RESOURCE PARTITIONING BY SAND DOLLARS IN CARBONATE AND SILICEOUS SEDIMENTS: EVIDENCE FROM PODIAL AND PARTICLE DIMENSIONS

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ABSTRACT

The sand dollars, *Leodia sexiesperforata* (Leske) and *Encope michelini* L. Agassiz, have overlapping geographical ranges and may co-occur in mixed flocks. *Leodia* is restricted entirely to biogenic carbonate sediments. *Mellita quinquiesperforata* (Leske), which has a similar geographical range to *Leodia,* occurs only on siliceous terrigenous substrates and the two species never co-exist. *Encope michelini* L. Agassiz occurs on both types of substrate. All three species are podial particle pickers, and use barrel-tipped podia, especially the long type surrounding the geniculate spine fields of the oral surface, for food collection. A typical mellitid of 100 mm diameter can have up to one million barrel-tipped podia. These podia have the same mean diameters in *Leodia* (71.6 ± 5.62 μm) and *Mellita* (71.8 ± 3.59 μm). The diversity of sizes is significantly greater in *Leodia.* The barrel-tipped podia of *E. michelini* are very much larger (104.4 ± 11.1 μm). The substrates inhabited by the three species have approximately 90% of their particles in the 100–400 μm range. Whereas *Mellita* is non-selective in collecting food particles, *Leodia* clearly selects small particles (50–200 μm) and shuns those above 200 μm. *Encope michelini* includes 26% of particles over 200 μm in its food grooves, but does not take those below 100 μm. Differences in feeding behavior thus provide a basis for resource partitioning between these sympatric species. They are discussed in relation to podial dimensions and spination, and compared with feeding behavior in *Mellita quinquiesperforata.*

INTRODUCTION

The feeding activities of sand dollars have been extensively investigated in recent years. It has become clear that many of them rely on oral surface podia for the selection of food material from the substrate. The tiny fibulariid, *Echinocyamus pusillus* (O. F. Müller), picks up diatoms, debris, or sediment particles and conveys them by podia to the mouth where they are chewed or scraped by the lantern teeth (Telford *et al.,* 1983). *Echinarachnius parma* (Lamarck) (Echinarachniidae) ingests sediment material without apparent selection of any particular size range, although diatoms are actively selected (Ellers and Telford, 1984). The lunulate sand dollar, *Mellita quinquiesperforata* (Leske) (Mellitidae), similarly collects sediment particles by means of oral surface podia and fractures them by action of the lantern teeth as they are ingested (Telford *et al.,* 1985). These studies all suggest that sand dollars feed in exactly the way that should be expected of an echinoid, despite their curious shape. These studies have directly challenged the former hypothesis of an aboral sieve mechanism proposed by Goodbody (1960).

In this paper we examine the feeding mechanisms of two more mellitid sand dollars, *Leodia sexiesperforata* (Leske) and *Encope michelini* L. Agassiz, which occur

in mixed flocks. Our purpose was to determine whether other members of this family use the same podial feeding mechanism and to explore the functional significance of differences in morphology of podia and spines. Two species living together might be expected to show differences in their use of the common food resource. Mooi (1986a, b) has described some differences between the podia of these species. In this paper we examine the relationship between podial dimensions and the size of sediment particles collected during the feeding process. This is the first published description of feeding in any species of *Encope* and the first re-examination of *Leodia sexiesperforata* since Goodbody (1960) proposed the sieve mechanism for that species. A direct comparison will be made between these two species, which live on biogenic carbonate sediments, and *Mellita quinquiesperforata,* which lives on terrigenous siliceous sediments.

Materials and Methods

Specimens of *L. sexiesperforata* and *E. michelini,* 50–110 mm in length, were collected in shallow water (3–15 m) off Long Key, Florida, during July, 1984, and maintained in running seawater with natural substrate in the laboratory. Observations of feeding and ciliary currents were made on live specimens using methods described elsewhere (Telford *et al.,* 1985). Several specimens were fixed in the field, in 10% formalin buffered in seawater, for analysis of gut and food groove contents. Six sediment samples of approximately 500 ml were collected from the surface (top 20 mm) in different places among the sand dollar flock. These were fixed in 10% buffered formalin to preserve living organisms and organic material. Larger samples were collected from time to time and kept fresh for use in holding tanks and for feeding observations. Additional specimens of *L. sexiesperforata* and substrate samples obtained from Eleuthera, Bahamas, in February, 1983, were preserved in the same way. Measurements of podia and distribution of podial pores in specimens of *E. michelini* and *L. sexiesperforata* collected at Torch Key, Florida (1982) were compared with specimens of *Mellita quinquiesperforata,* collected at Atlantic Beach, North Carolina (1982).

Specimens of the three species, from personal collections and those of the United States National Museum (USNM), were examined as follows (USNM catalog numbers in parentheses):

Leodia sexiesperforata: personal collections from Bahamas, Barbados, Florida Keys and Panama; USNM collections from Bermuda (E14495), Bahamas (E14892, E9009, #32651), Cuba (E10384), Dominican Republic (E14559), Puerto Rico (#19656), St. Thomas (E1183), St. Kitts (#7000), Windward Islands (E14560), Belize (#18932), Panama (#14579), Colombia (E14561), and Brazil (#5388).

Mellita quinquiesperforata: personal collections from North and South Carolina, Georgia, Atlantic and Gulf coasts of Florida; USNM collections from Virginia (#4980), Alabama (E15912, E15914, E15918, #25416-22), Louisiana (E6797), Texas (E6581-2, E5350), Panama (E14584), Colombia (E8091-2), Trinidad (E14062), Puerto Rico (E6608-11), and Brazil (E17195).

Encope michelini: personal collections from Long Key, Pigeon Key and Torch Key, Florida; USNM collections from South Carolina (E30005), Georgia (E29843-6), Gulf coast of Florida (#2185), Gulf of Mexico (E26711, E26714) and Brazil (E26706).

Podia (Mooi, 1986a, b) and spines (Telford *et al.,* 1985) were classified and the distribution of different types on the sand dollars was mapped. Isolated spines were measured by ocular micrometer; inter-spine distances were similarly estimated from

live and freshly killed specimens under a binocular microscope. Distribution of cilia on different spine types was examined by light microscopy of isolated spines.

Tip diameters of barrel-tipped podia were measured by eye-piece micrometer. Tissue was scraped away from the oral surface in ambulacra I, II, and III from four different specimens of each species, and mounted on a microscope slide. Diameters of 20 podia from each ambulacrum were determined. The data were pooled for each species and means and standard deviations calculated for the combined 240 measurements. Large specimens were chosen so that differences between species would not be obscured by size differences. Specimens of *E. michelini* ranged in size from 93.3 × 94.0 to 104.0 × 105.8 mm; *L. sexiesperforata* from 91.1 × 90.8 to 101.6 × 108.0 mm and *M. quinquiesperforata* from 92.8 × 97.8 up to 98.0 × 99.6 mm. Numbers of pores within the geniculate spine fields of these specimens were determined by cutting out small pieces of test and dissolving soft tissues in 5.25% sodium hypochlorite (commercial strength bleach). Cleaned pieces were dry-mounted on a slide and examined with transmitted light. The total number of podial pores in each of five fields of view in each ambulacrum (I, II, and III) was determined. The data were pooled for each specimen and the means calculated as number of podial pores per square millimeter of geniculate spine field. Estimates of total oral surface area and of the different spine fields were made by cutting out photographic reproductions of the sand dollars and weighing the individual areas.

Analyses of natural substrate, food groove material, and gut contents followed the methods developed by Ellers and Telford (1984) and by Telford *et al.*, (1985). Very small samples of substrate were strewn on glass microscope slides. All particles within several fields of view were drawn in outline by camera lucida after which length and width of at least 1000 from each sample were measured. Material from the food grooves was treated in the same way, but the sample sizes were somewhat smaller. Sediment grains were assigned to size classes 0–24, 25–49, 50–99, 100–199, 200–399, 400–799, and >800 μm and size-frequency histograms were constructed. The ϕ units used by geologists were not used because our interest centered on the numbers and size of sand grains and diameters of podial tips, not on sieve analyses of mass. However, our sediment analysis program also calculated the size-frequency distributions according to size classes for a standard sieve series, for purposes of comparison with other published data. Mean, standard deviation, and elongation (width/length) was calculated and the degree of angularity of the grains was estimated (Leeder, 1982). The significance of differences between particle size-frequency distributions of individual substrate samples and food groove samples was tested by Chi-square analysis, and between means by the t-statistic. All statistical procedures followed Sokal and Rolf (1981). Acid soluble carbonate was determined gravimetrically following digestion in HCl or EDTA.

RESULTS

Ciliary currents among the spines of *L. sexiesperforata* and *E. michelini* are similar to those already described for *M. quinquiesperforata* (Telford *et al.*, 1985). On the aboral surface two quite distinct patterns of flow occur. Within the petaloids, there is a central area of centrifugal flow. Between the respiratory podia, flow is directed from the center of the petaloid (ambulacrum) towards the outside (interambulacrum). Internally, coelomic fluid and cells flow from the outer to the inner pore of each podium, exactly counter to the external current. Around the petaloids, in the interambulacra, the respiratory flow is entrained in a general centrifugal current. Centrifugal flow appears to be diverted close to the lunules, so that their walls are washed by a downward flow within the depth of the spine field. It is easy to exaggerate the current towards

the lunules. Flow is usually visualized by means of suspended particles which may occur naturally (diatoms, etc.), or be introduced (*Artemia* eggs, black ink, etc.). Particles never describe a straight centrifugal trajectory. The spines are placed somewhat like the pins in a pinball machine. Suspended particles may be carried around a spine, or be driven to the right or left. Thus a group of particles will tend to fan out in the centrifugal flow and, inevitably, some will be carried passively towards the lunules. As in *M. quinquiesperforata*, most particles reaching the ambitus or passing via the lunules, are deposited into the sediment. There is a complex pattern of flow across the oral surface, which must be visualized in three dimensions. In the centers of the locomotory spine fields and the pressure drainage channels (Fig. 1) flow is centripetal but strongly divergent towards the margins of those zones, where it is deflected downwards. At the peristome small centripetal components remain and these unite in a downward flow beneath the mouth. There are some small differences in the flow patterns of *M. quinquiesperforata* and other species treated in this paper and they can be best attributed to differences in the relative sizes of the spine fields. Estimates of
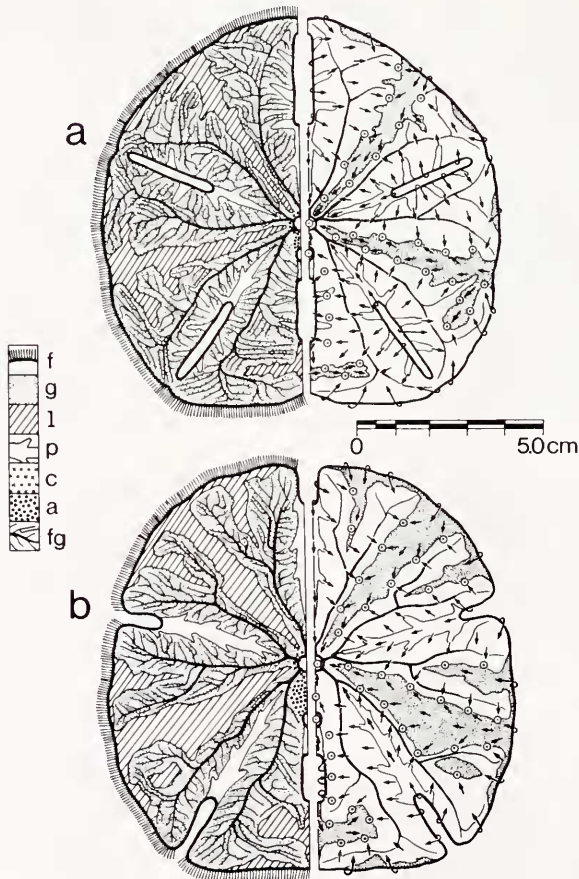

FIGURE 1. Distribution of spine types (left half) and ciliary currents (right half) on (a) *Leodia sexiesperforata* and (b) *Encope michelini*. For left half: f, fringe spines; g, geniculate spines; p, pressure drainage channel (pdc) spines; c, circum-oral spines; a, anal spines; fg, food grooves. For right half: arrows indicate direction of ciliary current flow; circles with central dot show convergence of currents with resulting downward flow to the substrate; locomotory areas stippled.

particle velocities in the ciliary currents were alike in all three species, ranging from 0.50 to 0.95 mm·s^{-1}.

In both *E. michelini* and *L. sexiesperforata*, aboral spination is very similar to that of *M. quinquiesperforata* (Telford *et al.*, 1985), but those of *Leodia* are more slender, those of *E. michelini* generally larger and more robust. The spines have the same orientations with respect to body axis, anterior to posterior size gradations and ratios of miliary to club-shaped spines. Spines of the oral surface are equally diversified into locomotory, geniculate, pdc spines, but in *Leodia* and *Encope*, the locomotory areas are relatively smaller and the geniculate areas correspondingly larger. In *M. quinquiesperforata* the locomotory spines occupy more than 30% of the aboral surface area, whereas in *E. michelini* and *L. sexiesperforata* they occupy only 25 and 20% of the surface, respectively. Interspine distances for *Leodia* and *Encope* are given in Table I. Locomotory spines in these two species are equally spaced but there are some differences in the spacing of geniculate and other spines. The ciliary currents described above are powered by diametrically opposed bands of cilia which extend for about 100 μm along the shaft of each spine from its base.

Barrel-tipped podia occur between the geniculate spines in all three species. In *E. michelini* the tip diameter is 104.4 ± 11.08 μm (n = 240); in *L. sexiesperforata* it is 71.6 ± 5.62 μm (n = 240) and in *M. quinquiesperforata* it is almost identical (71.8 ± 3.59), but *Leodia* has a significantly greater range of podial sizes ($P < 0.001$) (Fig. 2). The difference between *E. michelini* and the other two species is statistically significant ($P \ll 0.001$). There are highly significant differences between the densities of podial pores in these three species ($P \ll 0.001$) (Table II). Geniculate spine fields occupy approximately 75% of the total oral surface in *Leodia*, about 70% in *E. michelini*, and 65% in *Mellita*. Pressure drainage channels represent only about 5% of oral surface area in all three species.

Leodia sexiesperforata and *E. michelini* were collected from mixed flocks in shallow water, 5–10 m depth. They were always found on biogenic, carbonate sediments con-

TABLE I

Interspine spacing (μm) in Leodia sexiesperforata *and* Encope michelini

| | L. sexiesperforata | | E. michelini | |
Spine types	Space	±S.D.	Space	±S.D.
Locomotory-locomotory	303.0	30.2	297.8	38.2
Locomotory-miliary	190.4	26.5	180.0	35.7
Pdc-pdc	498.5	57.8	448.2	70.0
Pdc-miliary	214.8	33.8	240.7	63.3
Geniculate-geniculate	181.5	22.0	223.7	46.9
Anterior fringe-fringe	277.0	37.2	317.0	50.5
Posterior fringe-fringe	186.7	31.1	281.5	43.8
Anterior club-club	286.7	41.5	263.0	37.8
Anterior club-miliary	134.8	30.5	144.4	19.3
Anterior miliary-miliary	79.3	20.4	129.6	17.7
Posterior club-club	321.1	35.1	201.5	37.5
Posterior club-miliary	80.5	13.8	88.2	20.2
Posterior miliary-miliary	62.2	14.0	58.5	14.8
Anal lunule marginals	233.3	39.3	252.6	35.4
Lunular club-miliary	88.2	18.7	99.3	22.0
Lateral lunule marginals	189.6	33.5	—	—

Spaces given are mean distances between spine shafts immediately above the basal collar. For all measurements, n = 25.
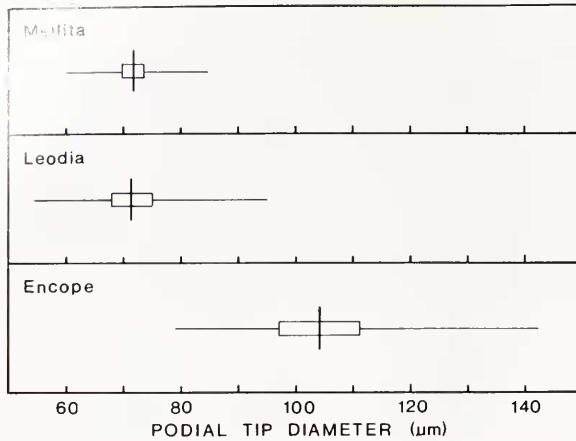
FIGURE 2.   Mean (vertical bar), standard deviation (box) and range of sizes (μm) (horizontal line) of short barrel-tipped podia in the geniculate spine fields of *Mellita quinquiesperforata, Leodia sexiesperforata,* and *Encope michelini.*

sisting of fragments of coralline algae (*Halimeda* etc.), shell, and coral debris. Approximately 90% of the particles were in the 100–400 μm range (Fig. 3), with a mean size of 213 ± 68.4 μm. The Eleuthera (Bahamas) sample, where only *Leodia* was found, had a lower mean grain size (158 ± 43.1) due to larger numbers of particles (23%) between 50 and 100 μm. *Mellita quinquiesperforata* occurs on terrigenous, siliceous sediments with a similar percentage of particles in the 100–400 μm range (Fig. 3) and a mean size of 186 ± 63.9. The remaining 10% of the *Mellita* substrate was less than 100 μm. In the biogenic sediment, 6% of the particles exceeded 400 μm. The mean elongation of the rather angular quartz sand grains was 0.70. The biogenic

TABLE II

Density of podial pores per mm^2 in the geniculate spine fields of Mellita quinquiesperforata, Leodia sexiesperforata, *and* Encope michelini

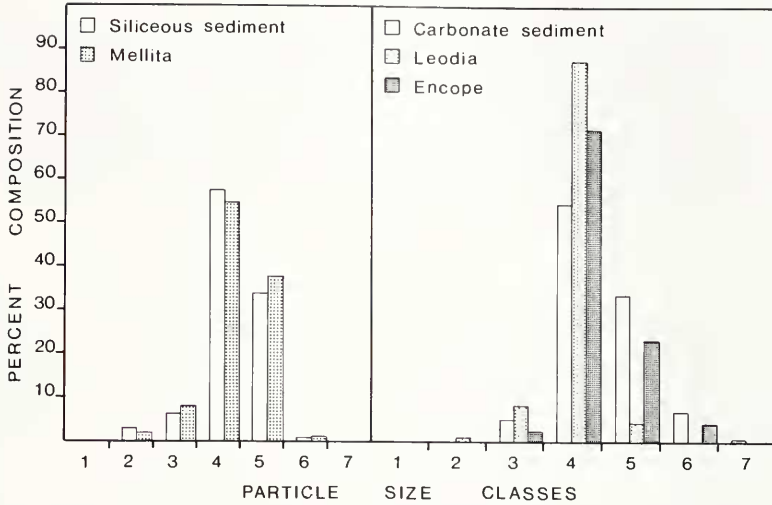|	Ambulacrum 1	Ambulacrum 2	Ambulacrum 3	Mean	S.D.
Mellita 1	140	168	180		
Mellita 2	136	173	167		
Mellita 3	147	170	178		
Mellita 4	144	168	183		
				163	±16.5
Leodia 1	115	139	143		
Leodia 2	111	136	146		
Leodia 3	120	135	150		
Leodia 4	109	134	140		
				132	±14.1
Encope 1	100	102	103		
Encope 2	98	107	99		
Encope 3	91	104	105		
Encope 4	95	99	102		
				100	±4.4

FIGURE 3. Particle size distributions in natural siliceous and carbonate sediments and food grooves of sand dollars inhabiting them. Mean particle size in the siliceous sediment was 186.2 ± 63.91 μm (n = 3109), and in the carbonate sediment 212.9 ± 68.43 μm (n = 3362). Within the food grooves, mean particle sizes were: *Mellita,* 181.7 ± 54.23 μm (n = 2735); *Leodia,* 140.8 ± 34.64 μm (n = 2969); *Encope,* 183.0 ± 88.52 μm (n = 2418).

grains were more rounded, distinctly subangular, with mean elongation of 0.72. Dissolution of small subsamples showed that this sediment was 100% carbonate. However, under the microscope occasional non-carbonate particles were observed. When the biogenic particles were dissolved carefully in 1–2% HCl or in EDTA, delicate organic "ghosts" of the grains became visible.

Leodia and *Encope,* like *Mellita,* are podial particle pickers. During feeding long barrel-tipped podia around the geniculate spine fields pick up individual sand grains which are then passed from podium to podium in an orderly progression towards the food grooves. As the particles are passed along, they can be held beneath the tips of the geniculate spines, in the space above the sediment, or they may pass between the tips of the spines, which are in constant motion during feeding. Upon arrival at the food grooves, the particles are moved centripetally towards the mouth by action of the food groove podia. Adhesion of particles and podia is at least partially due to a sticky glue-like substance (Thomas and Hermans, 1985). As the particles become coated with this material they readily adhere to each other and form cohesive strings in the food grooves. Analysis of the size-frequency distributions of particles in the food grooves (Fig. 3), shows that *Mellita* is non-selective: it collects particles in essentially the same proportions as they occur in the substrate. In the food grooves of *Leodia,* 87% of the particles were in the size range 100–200 μm, and the mean was 141 ± 34.6. Particles in the food grooves of *E. michelini* had a greater mean size (183 ± 88.5 μm). Differences between the mean sizes and the frequency distributions for these two species were statistically significant ($P \ll 0.001$). In both species, food groove material included a slightly higher proportion of forams and diatoms than observed in the native sediment. Particle size-frequency analysis of gut contents from *Leodia* and *E. michelini* was not possible by the methods used here. The contents included a large proportion of well pulverized sand grains, among a few larger particles. Some fragments were large enough to identify as broken forams, diatoms, and shell debris, but most of the material was amorphous and cohesive.

Fine material, such as particles of carmine and black ink (used for flow visualization), were deposited in the sediment around the ambitus. Those particles which were included in oral surface flow were brought to the edges of the locomotory spine fields where they were then deposited by downward currents. Some of this fine material adhered to podia and sand grains. As a consequence, some was included in the food groove material, still clinging to larger particles. We saw no evidence that this fine material was deliberately selected. In fact, most of it was left in the sediment.

DISCUSSION

Leodia sexiesperforata and *Encope michelini* have partially overlapping distributional ranges and often occur together in mixed flocks. *Leodia* ranges from North Carolina to Uruguay, including the Florida Keys, Bahamas, Greater and Lesser Antilles, and the Gulf of Mexico. *Encope michelini* is distributed from North Carolina south to the Florida Keys and throughout the Gulf of Mexico, but not in the Bahamas (Serafy, 1979). *Mellita quinquiesperforata* extends from Massachusetts to Florida, throughout the Gulf, Caribbean, Central and South America to Brazil, as well as all the Antilles (Serafy, 1979). From our own field experience and examination of museum material, it is apparent that *Leodia* occurs only on biogenic sands and that *Mellita* is restricted to terrigenous sediments. It is curious that this very striking feature of distribution has not been remarked upon previously. *Encope michelini* appears to inhabit both sediment types. In our own field studies we have only found this species on the biogenic sediments of the Florida Keys. However, examination of museum specimens from South Carolina, Georgia, elsewhere in Florida, and the Gulf of Mexico, showed mixtures of shell debris and substantial amounts of quartz grains in the food grooves.

The sediment particle sizes at the different collection sites were very similar. The mean particle size of siliceous material of Atlantic Beach (*Mellita*) is remarkably close to previously reported values for Bird Shoal, (180.8 ± 59.74) (Telford *et al.,* 1985) and for Florida (Serafy, 1979) ". . . fine quartz sand with modal grain size of 0.18 mm . . ." They are also quite comparable with the data reported by Weihe and Gray (1968) for their collecting sites in North Carolina. The mixed flocks of *Leodia* and *E. michelini* occur on a substrate incorporating a small but significant number of particles over 400 μm (6%), but otherwise very like the *Mellita* substrate. Many authors, including those already cited, have remarked on the scarcity of fine particles (<50 μm) in sand dollar habitats. The sediment analyses provided by Lane and Lawrence (1982) for a *Mellita* population near Tampa (Florida), showed 92% of the grains in the 125–250 μm size class, 5% in the 62.5–125 class, and the rest smaller than that. Our *Mellita* substrates did include 10% of the particles below 100 μm, but there was a substantial proportion over 250 μm (Fig. 3).

There are small differences in spination between the three species. On the aboral surface, the miliary sacs which fill the spaces between the tips of club spines, preventing the entry of particles during burrowing (Mooi, in press), are largest in *Mellita* and smallest in *E. michelini*. The generally centripetal ciliary currents remove the few small particles which drop through the protective canopy (Mooi, in press; Telford *et al.,* 1985). Interspine spacing on the aboral surface is wider in *Leodia* and *Encope* and the latter has wider spacing between the ambital fringe spines. On the oral surface, spacing between locomotory spines is widest in *Mellita* (460 ± 86 μm) but all other inter-spine distances are somewhat smaller. Within the geniculate spine fields *Mellita* has significantly more barrel-tipped podia per mm^2 (Table II) and *Leodia* likewise has more than *E. michelini*. These are the food gathering podia, which adhere to collected particles. Mean podial diameters reported here for *Mellita* (72 μm), based on large

numbers of measurements, are somewhat smaller than those reported by Phelan (1977) (84 μm) and much smaller than our own earlier reported value of 120 μm (Telford *et al.*, 1985) which, in retrospect, appears to represent an extreme and not the typical size of food gathering podia. In fact, these suckered podia in *Mellita* rarely approach 100 μm, even close to the peristome. *Encope michelini* has very much larger podia, none of them as small as the mean sizes for *Mellita* and *Leodia* (Fig. 2).

All three species use the impressively large numbers of podia on the oral surface for the collection and transport of food. *Leodia* has the most extensive geniculate spine areas and we estimate that individuals 100 mm in length have approximately 1 $\times$ 10^6 barrel-tipped podia, of which 150 $\times$ 10^3 are food collecting (long b-t) podia. *Mellita* has some 0.85 $\times$ 10^6 b-t podia (125 $\times$ 10^3 long) and *E. michelini* 0.70 $\times$ 10^6 (100 $\times$ 10^3 long). According to our estimates, the total area of the suckered podial tips in *Mellita* and *Leodia* represents over 40% of the total oral surface area and about 15% of this is the actual food collecting, long barrel-tipped podia. In *E. michelini* the total is even higher, about 60% of the total oral surface area, with a similar proportion of long b-t podia. Ciliary currents do not contribute significantly to the feeding process. As reported earlier (Telford *et al.*, 1985), *Mellita* is non-selective in its feeding. Both *Leodia* and *E. michelini* (Fig. 3) include disproportionately high percentages of the 100–200 μm fraction in their food grooves. *Leodia* also appears to select from the 50–100 μm class and to shun particles greater than 200 μm. *Encope michelini* takes very few particles less than 100 μm and includes significant amounts (26%) above 200 μm. Although one would not expect sand to be a limiting resource for these cohabiting sand dollars, some divergence of feeding and, hence, partitioning of the food resource appears to occur. Hammond (1982) concluded that sympatric holothuroids and echinoids in a similar habitat in Jamaica, did not show any resource partitioning: they all ingested sediment mixtures very similar to the composition of the surrounding sand. Although they are nonselective for particle sizes, Hammond (1983) did find evidence that some holothuroids and echinoids were selective for the organic content of grains. Ellers and Telford (1984) and Telford *et al.* (1985) found that feeding in clypeasteroids could be stimulated by presentation of diatom-enriched material, and both *Leodia* and *E. michelini* included relatively high proportions of forams and diatoms in the food grooves, suggesting that these were being actively selected. Scheibling (1980) found that microphagous feeding in the asteroid *Oreaster reticulatus* was similarly stimulated by the presence of diatoms, suggesting that selection of particles for nutrient content might, indeed, be widespread in deposit feeding echinoderms. The small differences in spination and the larger differences in podial dimensions and distribution, do not supply a ready mechanical explanation for resource partitioning by *Leodia* and *E. michelini*. It might be expected that species collecting larger particles would have wider spaces between the geniculate spines. This does not appear to be borne out by observation. The space between spine tips is constantly changing as the spines move and it is clear that *Mellita*, at least, is able to collect a mean particle size (180 μm) which is greater than the mean stationary inter-spine distance (150 μm). With podia very much like those of *Leodia, Mellita* nonetheless collects food particles more like the size range taken by *E. michelini*. It is possible that spacing between geniculate spines and podial tip dimensions together provide an upper limit to the size of particle handled. We suspect also that the podia are poorly suited to adhesion on particles substantially smaller than themselves and that this sets a lower limit. Certainly, the mean food groove particle sizes are 1.5 to 2.5 times the podial tip dimensions. In a comparison of *E. aberrans* and *E. michelini*, Phelan (1972) speculated that they might prefer different particle size ranges and noted that the dimensions of the food grooves and peristome differed. *Encope michelini* has wider, less distinct food grooves ($\sim$750

μm) than either *Leodia* or *Mellita* (~600 μm). Peristome diameters of *Mellita* and *E. michelini* (~3.75 mm) are significantly larger than *Leodia* (2.25 mm), in similar sized individuals. These dimensions are 15–20 times the mean linear dimensions of ingested particles. It is difficult to see how these peristome diameters might influence the size of particles selected as food. We would suggest that *E. michelini* and *Leodia* might tolerate wider sediment size ranges and particle size-frequency distributions. Both have greater podial size diversity than *Mellita,* which might allow them to handle a wider diversity of food particles. We suspect that *Leodia* overlaps the distribution of *E. michelini* only towards the upper and lower extremes of their respective particle tolerances. We can offer no explanation at present for the separation of *Mellita* and *Leodia* on different substrate types, both of which seem to be acceptable to *Encope* species.

When Goodbody (1960) examined stomach contents in *L. sexiesperforata* he was unable to identify much of the material but remarked on the small size of the particles. Until recently this has been one of the mainstays of the sieve hypothesis but Telford *et al.* (1985) concluded that the lantern of *Mellita quinquiesperforata* fragmented sand grains as they were ingested. Carbonate sand grains contain an organic matrix in which the calcite is originally deposited and, in addition, they are extensively penetrated by fine filaments of algae and sponges. It is this organic material which becomes visible under the microscope as an organic "ghost" of the sand grain following slow dissolving. They may thus be a more rewarding nutrient source than siliceous grains bearing only surface organics. The penetration by algae and sponges also makes these grains much more readily breakable by the lantern teeth. For this reason, sand grains ingested by *Leodia* and *E. michelini* are thoroughly pulverized into an unrecognizable paste, whereas the siliceous grains ingested by *Mellita* are broken into smaller but still recognizable granules.

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